

A new method for jointly assessing effects of climate change and nitrogen deposition on habitats



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ABSTRACT

Climate change and nitrogen (N) deposition are among the most important drivers of biodiversity change at a global scale. Although commonly considered separately in applied research, conservation, and policy development, both empirical evidence and modelling studies indicate that these two stressors may act synergistically and trigger a more pronounced biodiversity loss than each of them alone. Interactive effects thus need to be considered in biodiversity conservation. In this study, we propose a new method for jointly assessing risk from both stressors to habitats by combining climate envelope modelling and the evaluation of exceedance of empirical critical loads for eutrophication through N deposition. Based on this approach we can calculate a combined risk metric, which is the scaled exceedance of the N critical load and climatic thresholds in the three-dimensional space of N deposition, temperature, and water limitation. We use a habitat map to project this risk metric for 34 EUNIS habitat types across Austria. Resulting risk maps indicated that about 16 % of the area of these natural and semi-natural habitat types is currently at risk from either N exceedance, drought or warming. Using combinations of future climatic (RCP2.5 and RCP8.5) and N deposition (business as usual, current legislation and maximum feasible reduction) scenarios, we predict that the area at risk might increase to up to 19% until 2050, with risk from N-deposition decreasing and risk from climate change increasing. Combined impacts of both stressors affect only up to 2% of the entire evaluated area, but are much more frequent in particular habitat types such as oligotrophic bogs and subalpine to alpine grasslands. We conclude that this method provides a useful screening procedure to identify and compare areas and habitats under combined risk from both stressors and to thus support prioritization and decision making in biodiversity conservation.

1. Introduction

Biodiversity is under pressure globally from multiple drivers including land use change, overexploitation, climate change, atmospheric nitrogen (N) deposition, and other environmental stressors (Ceballos et al., 2015; Sala et al., 2000). Concern about the decline of biodiversity under these multiple threats and the consequences for ecosystem functioning and services has motivated considerable research effort (e.g. Barnosky et al., 2011; Bellard et al., 2012; Estes et al., 2011; Tittensor et al., 2014) as well as internationally coordinated policy

response (e.g. Convention on Biological Diversity, Intergovernmental Platform for Biodiversity & Ecosystem Services). Scenarios and projections of how biodiversity may change under plausible future pathways of drivers are key to proactive environmental policies and management (e.g. Guiot and Cramer, 2016; Pereira et al., 2010; Thuiller et al., 2013). A shortcoming of most of these projections is, however, that they exclusively consider one particular driver and neglect the simultaneous and possibly interacting effects of others (e.g. Pereira et al., 2010; Titeux et al., 2016).

Climate change and N deposition represent a pair of drivers that is

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known to have separate and interactive effects on biodiversity and ecosystems (Bernhardt-Römermann et al., 2015; Greaver et al., 2016; Porter et al., 2013). Adverse effects of N deposition mainly stem from eutrophication, which fosters the growth of opportunistic plant species and, eventually, the exclusion of less competitive ones (Bobbink et al., 2010a, 2010b; Gilliam, 2006; Hautier et al., 2009; McClean et al., 2011), and from acidification, which leads to cation imbalances, associated physiological stresses and loss of sensitive plant species from communities (Roem et al., 2002; Simkin et al., 2016a; Stevens et al., 2010). Both of these effects can propagate through the food web and alter the composition and diversity of heterotrophic groups (de Sassi et al., 2012; Wallisdevries and Van Swaay, 2006). Climate change may modify N supply to biota by influencing atmospheric N deposition through the amount and temporal pattern of precipitation, which in turn leads to modifications in soil chemical and microbial processes. Moreover, temperature and moisture conditions control the availability of soil N for plants via their effects on microbial transformation rates of reactive N (Butler et al., 2012; Guntiñas et al., 2012). Interactions are complex and only partly understood (Greaver et al., 2016), but both empirical observations and modelling studies indicate that a warmer and wetter climate may enhance detrimental effects of N deposition on biodiversity (Porter et al., 2013; Zavaleta et al., 2003) while a drier climate may render plant communities less sensitive to N effects because of reduced net N mineralization as well as reduced biological activity (Bobbink et al., 2010b; Simkin et al., 2016a).

Despite these potential interactions, the effects of climate change and N deposition have only recently begun to be considered together in large-scale assessments of their effect on biodiversity (De Vries et al., 2010). We assume that methodological issues have hindered such joint assessments. At larger spatial (and temporal) scales, the possible impact of climate change on biodiversity is mainly evaluated by means of species or habitat distribution models (SDMs) (e.g. Guisan and Thuiller, 2005; Thuiller et al., 2005). Spatial variation in N availability to biota cannot be easily mapped and, hence, is just emerging to be included into such models (Rowe et al., 2015). Instead, evaluations of biodiversity risk from N deposition for larger areas have mainly been based on the critical load (CL) approach, i.e. the definition of system or habitat specific thresholds beyond which negative effects on biodiversity, among other system attributes, are to be expected in the long run (Nilsson, 1988). This approach has, by contrast, not been applied in climate impact research and ‘climatic critical loads’ of habitats are hence not defined so far.

As a step forward to bridging the gap between these different metrics, we present a method to express future threats to biodiversity from N deposition and climate change on a common scale. We therefore adapt the CL approach by defining critical ‘climatic loads’, or – more accurately – climatic thresholds of ecosystems. We derive these climatic thresholds from SDMs of the species that typically occur in these ecosystems. The risk of an ecosystem from either climate change or nitrogen deposition can then be compared in terms of exceedance of the CL for N and the climatic threshold, respectively, and a combined risk from the exceedance of both thresholds can be calculated. We emphasize that the aim of our approach is not to improve mechanistic understanding of the interactive effects of climate and N deposition on biodiversity. Rather, we want to provide a consistent screening procedure to identify and compare areas and habitats under risk from both of these components of global environmental change. We illustrate the method by an application to the natural and semi-natural habitat types of Austria.

2. Material and methods

2.1. Conceptual approach

The exceedance of system-specific CL of airborne pollutants has been quantified by critical load functions which provide distances

between measured deposition values and potentially interdependent effect thresholds in one or more dimensions (Posch et al., 2001). These thresholds, i.e. the CLs of habitat types, are derived by syntheses of experimental and observational studies (e.g. Bobbink et al., 2010a, 2010b). Whether and how much deposition exceeds the CL can be mapped in geographical space by combining ecosystem or habitat maps with deposition maps (e.g. Henry and Aherne, 2014; Posch et al., 2015). Here, we transfer this approach to climate impact evaluation by defining analogous ‘critical loads of climate’ for habitat types, henceforth called climatic thresholds. We then overlay both climatic maps and N-deposition maps with habitat maps to produce a map of combined climatic and N deposition exceedance.

Our definition of climatic thresholds for particular habitat types is based on the idea that such habitat types can be characterized by the co-occurrence of a set of ‘characteristic’ species which are special to or especially abundant under the environmental conditions typical for these habitats. This idea underlies the phytosociological approach to habitat classification (Dengler et al., 2008) which is, in turn, the basis of the conservation-oriented legislation and administration in the European Union (e.g. Habitat Directive, Directive 92/43/EEC; Rodwell et al., 2002). The close relationship between the typical environmental conditions and the characteristic species of a habitat type (Willner et al., 2009) implies that the climatic niche of a habitat type can be derived from the climatic requirements of its characteristic species.

SDMs have been specifically developed for quantifying species’ realized niches from geographical distribution patterns (Franklin, 2010). The predictions of an SDM relate species’ occurrence probability to one or more ecological gradients. Here, we use this modelling technique for defining a climatic threshold of a particular habitat type by (1) projecting occurrence probabilities of all of the characteristic species of this habitat type into a two-dimensional (mean annual temperature, annual precipitation sum) climatic space; (2) calculating, from these projections, the average occurrence probability of all characteristic species for each XY-value in this climatic space; and (3) defining a threshold of this averaged occurrence probability below which decline or loss of characteristic species, and hence significant habitat

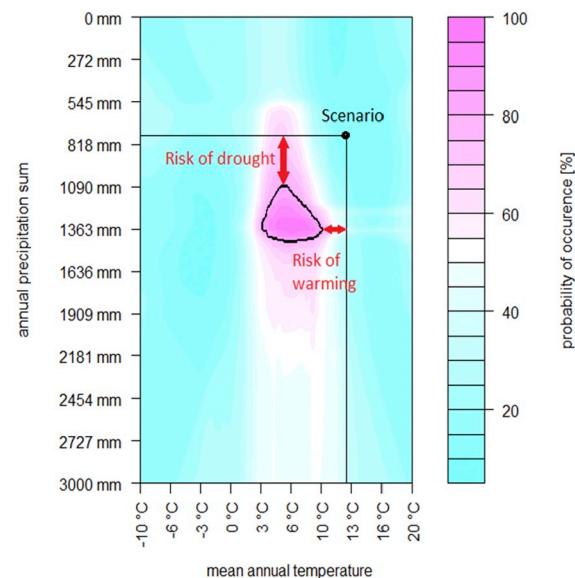


Fig. 1. Representation of the niche of a habitat type (Fagion sylvaticae = European beech forests) in temperature-precipitation space. Colours represent probability of occurrence as calculated from averaging SDM projections of all characteristic plant species of the habitat type. The black line delimits the climatic niche as defined by an averaged probability of occurrence of characteristic species of 80%. The precipitation axis was reversed as we assumed drought stress to be a more important challenge for Austrian plants under climate change than excess of water.

alteration, is to be expected. The climatic exceedance, or the climatic risk for a particular habitat at a particular site in the real-world landscape can then be calculated as the two-dimensional Euclidean distance of the temperature and precipitation values at this site and the climatic (=temperature and precipitation) thresholds of the respective habitat type (cf. Fig. 1).

2.2. Study area

The study area covers Austria, a landlocked country of Central Europe spanning approximately 84,000 km². The mean annual temperature in Austria ranges between -9°C at the highest peaks of the Alps and 10°C in the Eastern lowlands, and the annual precipitation sum between a minimum of approximately 500 mm and a maximum of 2100 mm (www.worldclim.org). High climatic diversity is mainly due to the rugged terrain and elevational gradient of the Austrian Alps, which cover about two thirds of the country and are responsible for the high habitat diversity.

2.3. Climatic data

Spatial variability of current climatic conditions in Austria was mapped on a $100 \times 100\text{ m}$ raster by statistically downscaling WorldClim maps (<http://worldclim.org/>, original resolution $30'' \approx 1\text{ km}^2$ in Austria) of monthly temperatures and precipitation sums to this spatial resolution. Downscaling was done by analysing the correlation of temperature and precipitation to elevation by means of running window regression (Dullinger et al., 2012; Zimmermann et al., 2009). The mean annual temperature and annual precipitation sum was then calculated from these downscaled monthly values for each cell of the $100 \times 100\text{ m}$ raster.

Maps of the same two climatic variables were calculated for two scenarios of the most recent IPCC report (IPCC, 2014), the representative concentration pathways RCP2.6 and RCP8.5, corresponding to the mildest and most severe climate change scenario, respectively. Data of these climatic scenarios for the years 2030 (average 2014–2046) and 2050 (average 2034–2066) were taken from the Cordex portal (<http://cordexesg.dmi.dk/esgf-web-fe/live>, spatial resolution $11'$, downloaded in May 2015) and downscaled to $100 \times 100\text{ m}$ raster maps of future mean annual temperature and annual precipitation sums using the same methods as for current climatic maps.

2.4. Selection of habitat types

As our focus was on biodiversity conservation, we concentrated on natural and semi-natural habitat types of Austria. More specifically, we included the following habitats: mires (raised and blanket bogs, valley mires, poor fens and transition mires, base-rich fens and calcareous spring mires), heaths (dry heaths, alpine, subalpine and arctic scrub), alpine and subalpine grasslands, dry, wet and extensively used mesic grasslands, broad-leaved forests, and conifer forests (Appendix: Table 1). We distinguished the respective habitat types and extracted their characteristic species following the syntaxonomical system of Austrian plant communities (Mucina et al., 1993; Willner and Grabherr, 2007). In total, the above broad habitat types are represented by 80 alliances of this syntaxonomical system in Austria, defined by a total set of 742 characteristic vascular plant species. Due to data restrictions (see below) we reduced this set to 482 species representing 66 alliances.

2.5. Species distribution data

To cover the climatic niches of the characteristic species, or the alliances they represent, as completely as possible we used a set of 70,780 vegetation plot records covering most parts of eastern, western and southern Europe. Records represent complete lists of vascular

plants growing in plots of variable sizes ($\sim 5\text{--}500\text{ m}^2$). The data were provided by databases (Appendix: Table 2) participating in the European Vegetation Archive (EVA) (Chytrý et al., 2016). All plots were geo-referenced, mostly at an accuracy of $< 1\text{ km}$. Because these data were drawn from different original sources, we merged the respective species lists by standardizing species names using the taxonstand package (Cayuela and Oksanen, 2016) in R version 3.1.1 (R Core Team, 2017) and subsequent manual control of possibly unresolved taxonomic problems.

2.6. Species distribution models (SDM)

SDMs were calibrated for the 482 characteristic species which were sufficiently frequent (> 20 occurrences) in the 70,780 vegetation plots. Models used presence-absence of a species in the plots as the dependent variable and mean annual temperature and annual precipitation sum as the independent variables. We used the original $30''$ -WorldClim data for model fitting. SDMs were calibrated in biomod2 (Thuiller et al., 2014) using an ensemble of modelling techniques which commonly outperforms any single technique (Araujo and New, 2007). We therefore selected a mix of regression based and machine-learning techniques, namely Generalized Linear Models (GLM), Generalized Boosted Regression Models (GBM), Generalized Additive Models (GAM) and Multivariate Adaptive Regression Splines (MARS). These techniques have complementary strengths and were among those producing most accurate projections in comparative studies (Elith et al., 2006; Guisan et al., 2007). For each technique we used three replicate runs. In each run, a randomly selected subset of 70% of the plots was used for calibration and the remaining 30% for model evaluation. Calibrated models were then used to project each species' probability of occurrence into the two-dimensional climatic space (cf. Fig. 1) using an ensemble forecasting approach. Thereby, the projected probability of occurrence at a particular combination of mean annual temperature and annual precipitation sum represents a weighted average of the projections of each single model (GLM, GBM, GAM, MARS), with ROC-scores of the models used as weights. Models with a ROC-score < 0.7 were excluded from the ensemble forecast (Appendix: Table 3).

Projections for all characteristic species of a habitat type were subsequently stacked and occurrence probabilities averaged (cf. Fig. 1). Because projected probabilities numerically depend on species frequency in the dataset and the statistical modelling method applied, we standardized these probabilities to $[0,1]$ for each species beforehand to remove any such bias and guarantee equal impact of each species on the averaged occurrence probability. For further analyses, we then defined a threshold value of the averaged occurrence probability below which we assumed that long-term persistence of the respective habitat type is impossible because climatic conditions do not match the climatic requirements of its characteristic species. This threshold approach is hence analogous to the definition of CLs of N deposition. The selection of the probability threshold in climatic space was arbitrary because data for estimating an optimal value were not available. To incorporate uncertainty from this arbitrary choice, we based all subsequent calculations on three different such thresholds, namely: (1) $p = 0.7$ or (2) $p = 0.8$ or (3) $p = 0.9$. The lower the threshold, the lower the probability that a certain magnitude of climate change will result in an exceedance of the habitat's climatic threshold at a particular site in the real-world landscape, i.e. the less sensitive the metric is to possible impacts of climate change on the respective habitat type.

2.7. Data on N deposition

We downscaled the effective European Monitoring and Evaluation Programme -Meteorological Synthesizing Centre - West (EMEP-MSCW) N deposition data (Simpson et al., 2012) with a resolution of $50 \times 50\text{ km}$ to $0.1 \times 0.05^{\circ}$ Lat/Lon resolution using precipitation data and a digital elevation model. Precipitation was taken from Isotta et al.

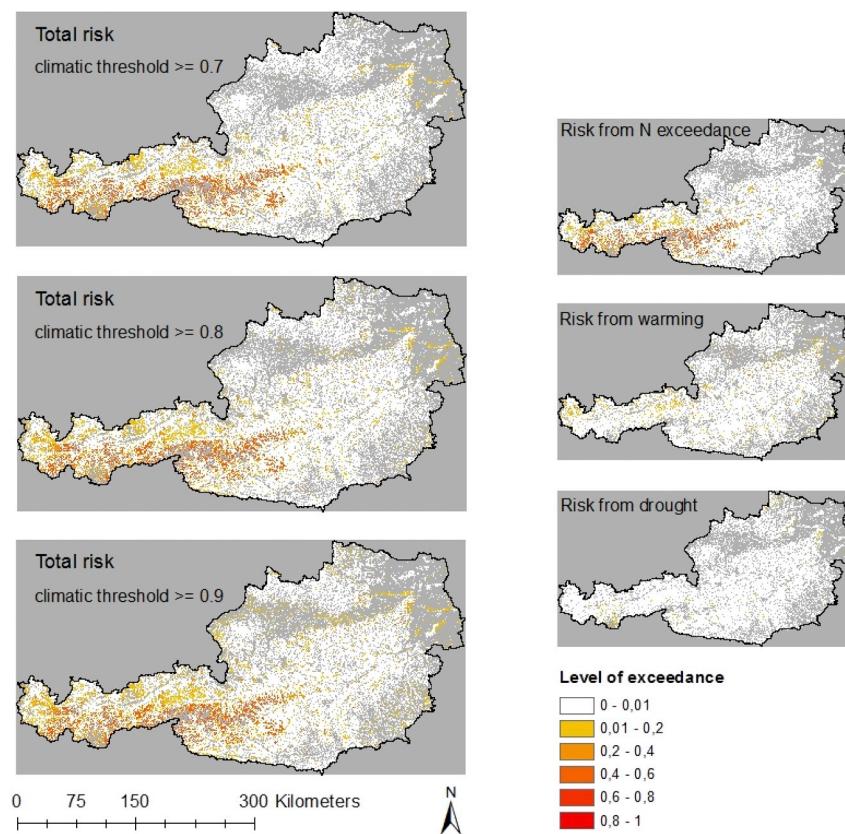


Fig. 2. Maps of risk from nitrogen deposition, rise of temperature and drought, i.e. exceedance of CLs or climatic thresholds for 66 natural and semi-natural habitat types in Austria in the year 2050, computed for a combination of RCP8.5 climate and B10 N-deposition scenarios. Climatic risk calculations were done for three different climatic thresholds representing different assumed sensitivity of habitat types to warming and drought ($p = 0.7$, $p = 0.8$ and $p = 0.9$). Risk levels were standardized to [0,1] for each of N deposition, temperature and drought separately, with 0 indicating no risk and 1 indicating maximum risk. Total risk is the three-dimensional Euclidean distance between predicted values of N-deposition, temperature and precipitation and the CL or climatic thresholds of the habitat type mapped at a site, respectively. Areas where none of the modelled habitat types occur are given in grey and have not been evaluated (further maps in Appendix, Fig. 6).

(2014), who provide a daily precipitation dataset for the Alpine region (resolution 5×5 km). Annual mean precipitation sum for the period 1979 to 2008 was calculated from this data and spatially interpolated to the $0.1 \times 0.05^\circ$ Lat/Lon target resolution. The mean elevation of each cell of the $0.1 \times 0.05^\circ$ Lat/Lon grid was calculated from a 70×70 m digital elevation model. Since N deposition increases with precipitation, the coarse scale deposition data were scaled with the finer scale precipitation data: areas with lower precipitation in a coarse scale cell received less deposition and vice versa, while the mass balance was maintained. Additionally, we took into account elevational effects because of the high variation of elevation within the coarse scale grid cells. Above 1000 m a.s.l. N ion concentrations in wet deposition increase by 2.5% per 100 altitudinal meters whereas below 1000 m concentrations they are independent of elevation (Schneider, 1998). These rules were used to downscale wet N deposition whereas dry deposition was taken from the coarse scale grids as they were.

We used three different N deposition scenarios for the years 2010 and 2030 which were provided by the European Coordination Centre for Effects (RIVM, NL, see <https://wge-cce.org/>) using the latest EMEP model version (Simpson et al., 2012): i) the current legislation (CLE) scenario with revised Gothenburg Protocol emissions until 2030, ii) the technically maximum feasible emission reduction scenario (MFR) until 2030, and iii) the 2010 deposition values as baseline with no further reduction (B10). In all scenarios, N deposition for the year 2050 was assumed to be the same as for 2030, since currently available N deposition scenarios only project until 2030.

2.8. Cross-walking syntaxonomical alliances with EUNIS habitats

CLs of N for European habitats are defined for habitat types of the European Nature Information System (EUNIS, <http://eunis.eea.europa.eu/>), but not for alliances of the syntaxonomical system. Moreover, the available 100×100 m habitat map of Austria also uses the EUNIS classification system (Dirnböck and Peterseil, 2013). We hence

classified the 66 alliances into a total of 34 EUNIS habitat types and then used the CLs of the latter for the alliances assigned to them. Thereby, some alliances were classified into several different EUNIS habitat types, either because they are more broadly defined than any particular EUNIS habitat type, or because they don't exactly match one particular EUNIS habitat. In such cases, an alliance was assigned the average CL of all the corresponding EUNIS habitat types. By contrast, some EUNIS habitat types included more than one alliance. In this case, we assigned all the respective alliances the same CL of the respective EUNIS habitat type (Appendix, Table 1).

2.9. Risk maps

Based on the different climatic and N deposition thresholds, the N deposition and climate change scenarios, and the 100×100 m habitat map of Austria (Dirnböck and Peterseil, 2013), we computed risk maps separately for temperature, drought and N deposition. Risk was thereby defined as the magnitude by which N deposition, temperature, or precipitation predicted for a particular 100×100 m cell exceeds the empirical CL for N (taken from Bobbink and Hettelingh, 2011) or the calculated climatic threshold for temperature or drought, respectively, of the habitat type present at this 100×100 m cell according to the habitat map. Climatic exceedance was calculated under all three threshold values of averaged occurrence probability of characteristic species ($p = 0.7$, $p = 0.8$ and $p = 0.9$) as described above.

By scaling the calculated range of exceedance values to [0,1] for each of N, temperature and drought, we subsequently re-aligned them on a relative scale and removed effects of different measurement units. The scaled exceedance values were then combined into a joint risk metric by calculating the three-dimensional exceedance as the Euclidean distance between values of temperature, precipitation and N deposition predicted for a 100×100 cell and the respective thresholds (non-exceedance entered the calculation as zero-distance). We henceforth call this metric 'total risk'. To keep this risk metric conservative,

we generally assumed that EUNIS-habitat types to which several taxonomical alliances have been assigned are represented at a particular 100×100 m cell of the map by the alliance with the lowest respective risk value.

Since the total risk index does not reveal if one, two or all three stressors pose a threat, we furthermore defined ‘combined risk’ as simultaneous risk of at least two stressors within a cell.

2.10. Risk differences among scenarios, climatic thresholds and habitat types

We evaluated differences in area at total risk among climatic and N deposition scenarios and among different climatic thresholds. Statistical significance of these differences was tested by means of logistic regression models on the basis of 50 random samples per possible combination of N deposition and climatic scenarios. One sample comprised 1000 randomly selected 100×100 m cells of the map. The number of cells with a total risk value > 0 in each sample was the dependent variable of the regression, and the scenario combination was the factorial independent variable.

In order to gain more specific information on habitats, we also calculated the percentage of area of EUNIS habitat types affected by combined and single risks.

3. Results

3.1. Magnitude of risk

The full factorial combination of three N-deposition scenarios, two climate change scenarios, two time horizons (2030 and 2050) and three different climatic thresholds yielded a total of 36 different future risk maps for Austria (see Fig. 2 below as an example).

For both 2030 and 2050, the average magnitude of risk from N deposition across Austria, i.e. the average magnitude of exceedance of the CL is considerably higher than the average risk from temperature or drought, i.e. the magnitude of exceedance of the respective climatic thresholds (Fig. 2). As a consequence, total risk maps are dominated by N-risk (Fig. 2). This result holds even when the most severe climatic

scenario (RCP8.5) is combined with the lowest N-deposition scenario (MFR). Risk from N deposition significantly declines under both CLE and MFR as compared to B10 (Appendix, Fig. 7b). As a result, (1) the average total risk across all climatic and N deposition scenarios is projected to decline in the future (Appendix, Fig. 7a); and, (2) if we focus on a particular N-scenario, differences in total risk between the two climate change scenarios are negligible (Appendix, Fig. 7c).

3.2. Area at risk

The area affected by total risk, i.e. the number of 100×100 m cells where at least one of CL and the climatic thresholds of temperature or drought, respectively, are exceeded, increases until 2050 (2010 to 2050, $p < 0.01$ and 2030 to 2050, $p < 0.01$, cf. Appendix, Table 4). This increase is the greater the more severe the climatic scenario (Appendix, Fig. 8, Table 4). Indeed, risk from drought and temperature make up for at least half of the area at total risk in 2050 under the severe RCP8.5 scenario, while risk from N deposition dominates the area at total risk under the current climate. (cf. Fig. 3). Under the combination of N deposition and climatic scenarios, magnitude and area of total risk are hence predicted to develop in opposite directions during the decades to come: while the expected decrease in N-deposition lowers the average magnitude of total risk, predicted climate change expands the area under total risk in Austria. Regarding climatic factors individually, the area at risk from warming is increasing with severity of the climate scenario and with time, whereas the area at risk from drought is decreasing by 2050 in both the RCP2.6 and RCP8.5 scenarios (Fig. 3). As a corollary, the predicted expansion of the area at total risk until 2050 is driven by temperature change alone. In addition, and as expected, the area at risk is also larger if the climatic threshold, i.e. the critical average occurrence probability of the characteristic species of a habitat type, is set to a higher value (Appendix, Fig. 8 and Table 4).

Although total risk affects up to 19% of all evaluated area, combined risk of two or all three stressors simultaneously is only found in up to 2% of all cells, depending on the scenario. Simultaneous risk from warming and N exceedance or from drought and N exceedance, respectively, is more frequent than simultaneous risk from drought and

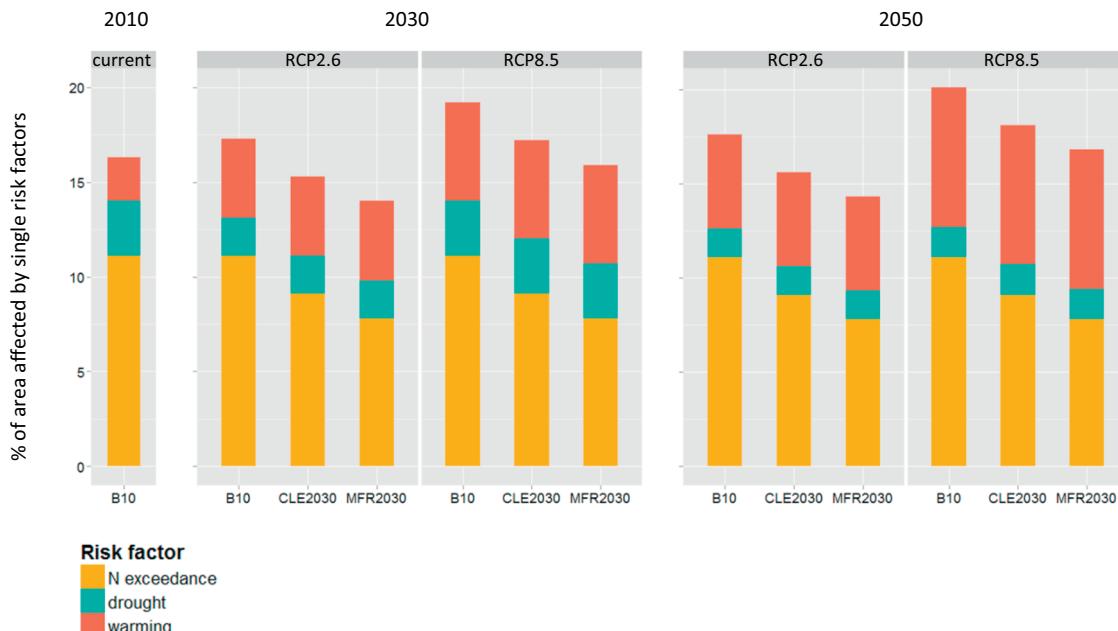


Fig. 3. Percentage of the Austrian area evaluated in this study where at least one of 66 natural and semi-natural habitat types is affected by exceedance of CL of N-deposition or of climatic thresholds for warming or drought, respectively for different years and under different combinations of climate change and N-deposition scenarios. For explanation of scenarios codes see text.

Areas of combined risk and its distribution among habitats

2050

Climate scenario = RCP8.5
N deposition scenario = B10

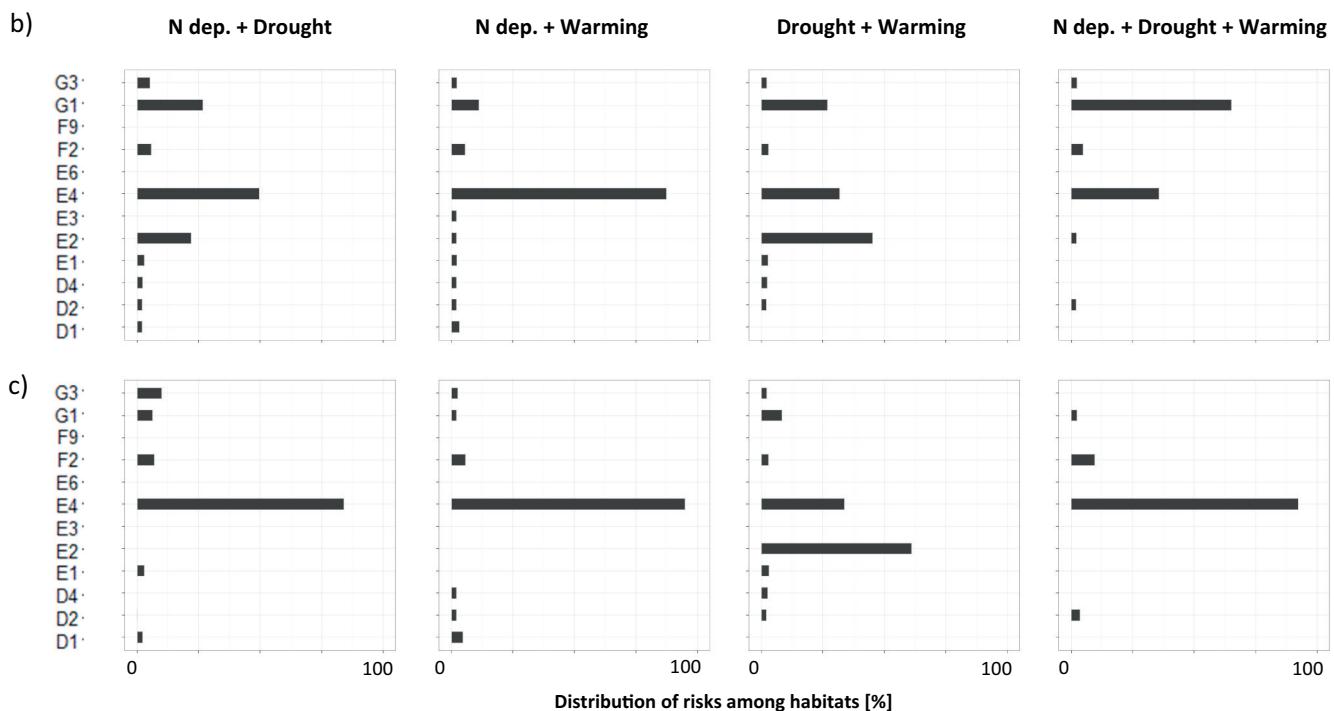
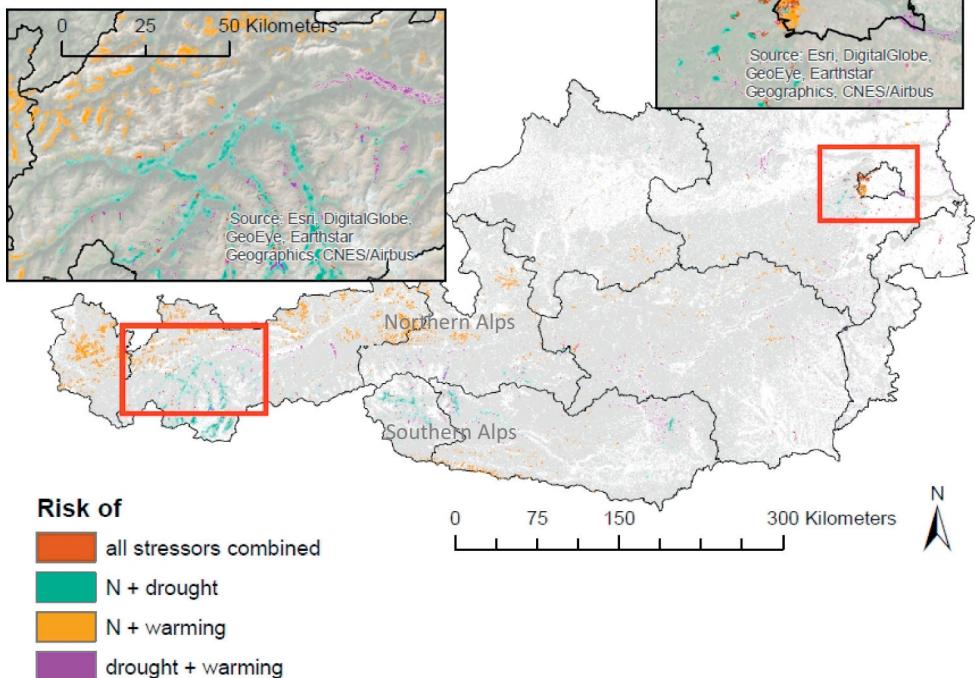
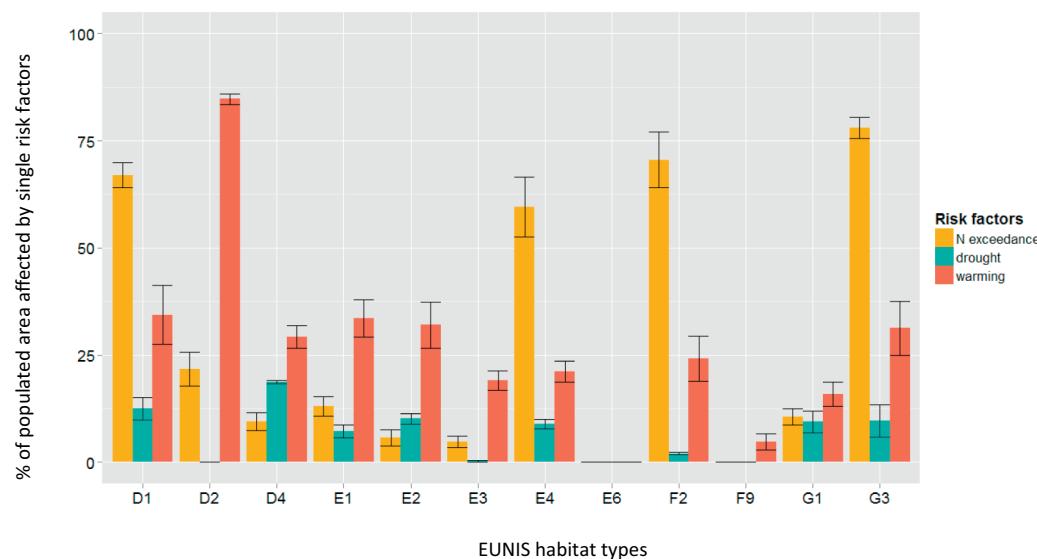


Fig. 4. Map of combined risks in 2050 calculated with the scenario combination of RCP8.5 and B10. Two areas with relatively high levels of combined risks are zoomed for purpose of illustration (a). Distribution of cells under combined risks in 2050 among EUNIS habitat types under the “worst” (RCP8.5 and B10) (b) and the “best” (RCP2.6 and MFR) case scenario combinations (c). Codes represent habitat types according to level 2 of the EUNIS classification: [D1] Raised and blanket bogs; [D2] Valley mires, poor fens and transition mires; [D4] Base-rich fens and calcareous spring mires; [E1] Dry grassland; [E2] Mesic grassland; [E3] Seasonally wet and wet grassland; [E4] Alpine and subalpine grassland; [E6] Continental inland salt steppes; [F2] Arctic, alpine and subalpine scrub; [F9] Riverine and fen scrubs; [G1] Broadleaved deciduous woodland; [G3] Coniferous woodland.



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warming. Warming and N risk are often combined in the northern parts of the Austrian Alps, whereas N exceedance and drought risk mostly co-occur in the southern and western parts of Austria (cf. Fig. 4a). Combined risk of all three stressors was modelled to occur in as little as 0.8% (“worst case scenario”) of Austria (cf. Fig. 4a).

3.3. Differences in populated area at risk among habitats

With regard to individual factors, N deposition particularly puts ‘Raised blanket bogs’, ‘Alpine and subalpine grassland’, ‘Arctic, alpine and subalpine scrub’ and ‘Coniferous Woodland’ at risk. Averaged over all scenario combinations, CLs of these habitat types are exceeded at 60–80% of their current ranges in Austria (Fig. 5). ‘Valley mires, poor fens and transition mires’ appear particularly threatened by warming with an exceedance of the respective climate threshold at 85% of its area on average across scenarios. Moreover, ‘Raised blanket bogs’, ‘Dry grassland’, ‘Mesic grassland’, and ‘Coniferous woodlands’ also experience high risk of warming (Fig. 5). Risk of drought is less widespread, affecting approximately 19% of ‘Base-rich fens and calcareous spring mires’, and 10% of the area of ‘Broadleaved deciduous woodland’, ‘Coniferous woodlands’, ‘Mesic grassland’ as well as ‘Raised and blanket bogs’.

‘Alpine and subalpine grassland’ is the habitat most frequently affected by two stressors in combination (Fig. 4b–c). In both “best” (RCP 2.6 and MFR scenarios) and “worst” (RCP 8.5 and B10 scenarios) case scenario combinations, > 87% of cells with simultaneous negative effects of N exceedance and warming are found in areas covered by this habitat type (Appendix, Table 5). In turn, 8 to 21% of the total area of this habitat type is affected by this combination of risk factors (Appendix, Table 5). Risk of N exceedance in combination with drought is also mainly found for alpine and subalpine grasslands, but affects a much lower percentage of this habitat type (2–4%, Appendix, Table 5). In terms of the area covered by a habitat type, the combination of N and warming threatens ‘Raised and blanket bogs’ most severely (43 and 52% of the total area of this habitat type in Austria for the “best” and “worst” scenario combinations, respectively, cf. Appendix, Table 5).

Most cells with a combined risk of drought and warming are currently covered by habitat types ‘Alpine and subalpine grassland’ and ‘Mesic grassland’. However, this combination affects < 2% of the total area of these two habitat types. In terms of area affected, simultaneous risk from warming and drought threatens ‘Base-rich fens and calcareous spring mires’ (9%–11% of the area covered by this habitat type in

Fig. 5. Mean percentage of the area covered by different EUNIS habitat types in Austria where N deposition, temperature or drought are predicted to exceed the CL of N, or the climatic threshold for warming or drought, respectively, in the year 2050. Bars represent averages from calculations that are based on all possible combinations of two climate change and three N deposition scenarios, error bars indicate standard deviations. Calculations are based on climatic thresholds set to $p = 0.8$ (see text for details). Codes represent habitat types according to level 2 of the EUNIS classification: [D1] Raised and blanket bogs; [D2] Valley mires, poor fens and transition mires; [D4] Base-rich fens and calcareous spring mires; [E1] Dry grassland; [E2] Mesic grassland; [E3] Seasonally wet and wet grassland; [E4] Alpine and subalpine grassland; [F2] Arctic, alpine and subalpine scrub; [F9] Riverine and fen scrubs; [G1] Broadleaved deciduous woodland; [G3] Coniferous woodland.

Austria) and ‘Broadleaved deciduous woodland’ (2–11%) most severely (Appendix, Table 5).

Combined risks from all three stressors are rare. Under the “worst” scenario combination (B10 & RCP 8.5), ‘Broadleaved deciduous woodland’ is the only habitat type appreciably affected (9% of its total area, Appendix, Table 5).

4. Discussion

The method we present here combines current state-of-the-art assessment tools in climate change and N deposition impact studies into a common framework. The approach was not aimed at improving our mechanistic understanding of interactions between climate and N deposition on biodiversity, but as a screening procedure to identify areas and habitats under risk from both. Its application to Austria demonstrates that currently between 13 and 16% of the area of natural and semi-natural habitat types (mires, heaths, alpine grasslands, dry, wet and extensively used mesic grasslands, broad-leaved and near-natural conifer forests) are exposed to either an exceedance of N deposition, climate warming, drought or a combination of these stressors. We further show that areas exposed to risk from at least two of these factors simultaneously are covering only up to 2% of the total area evaluated, but a much higher percentage (up to 50%) of the range of some particular habitat types, especially alpine grasslands and mires. Risk from N deposition is dominating the current situation (year 2010) as compared to climate induced risks. The average magnitude of total risk, i.e. the average magnitude of exceedance of CLs and/or climatic thresholds per 100×100 m cell, is predicted to decrease in the future due to lower N deposition in the applied scenarios. By contrast, the size of the area exposed to risk from the three factors evaluated increases as a result of accelerating climate change. To put it in a different way, the relative impacts of N deposition and climate are predicted to change in the future, with threat from N deposition decreasing (from a currently high level) and threat from climate change increasing (from a currently low level). Nevertheless, until 2050 exceedance of CLs of N deposition still affects nearly as large areas and is of higher average magnitude than exceedance of climatic thresholds under all scenario combinations. This domination of N deposition over climate related effects is likely due to the relatively short time horizon we used for our simulations. Beyond 2050, climate effects on biodiversity will probably become more severe. As an example, the RCP8.5 scenario predicts a 4-fold warming by 2100 as compared to the period until 2050 (Knutti and

Sedláček, 2012). In addition, it may be that the CL of N deposition is more sensitive than our SDM-derived climatic thresholds because the former focuses on “significant harmful effects on [any] sensitive elements of the environment” (Bobbink et al., 2010a, 2010b), whereas the latter is based on the match between a site's climate and the requirements of not just one but of the ‘average species’ characteristic to the respective habitat type.

Combined risk of warming and N deposition exceedance was found in the northern alpine region, and combined risk of drought and N exceedance was found in the southern Alps of Austria. This spatial segregation of risks is a result of the climatic north-south gradient across the Alps from a temperate to a sub-Mediterranean climate (Beniston, 2005), and of climate change scenarios that propose decreasing precipitation (especially in summer) in the southern Alps, but less so in the northern Alps (Heinrich et al., 2013). Evidence is increasing that European alpine plant communities have already responded to recent environmental changes with climate warming being the factor most discussed so far (Gottfried et al., 2012; Pauli et al., 2012; Vittoz et al., 2009). However, N deposition may have actually contributed to the observed changes. Indeed, the northern and southern Alps are exposed to the highest N deposition loads in Austria (Rogora et al., 2006), alpine habitats tend to have low empirical critical loads (Bobbink and Hettelingh, 2011), and recent observations have demonstrated that species with marked elevational range change during the recent decades are often those with high nutrient requirements, at least in mountain grasslands (Rumpf et al., 2018). Moreover, negative effects of either short-term high or long-term low doses of N deposition on the diversity of these grasslands are experimentally well documented (Humbert et al., 2015). Humbert et al. (2015) also suggested that with climate warming the effects of N deposition may be exacerbated because N deposition causes more diversity loss in warmer climates (cf. also Simkin et al., 2016b). Indeed, warming causes faster mineralization of N, particularly under higher precipitation and soil moisture. However, higher frequency and strength of drought events may offset nutrient turnover in soils (Rennenberg et al., 2009) and may hence compensate negative effects of N deposition, particularly on calcareous soils (Diekmann et al., 2014). Such an offsetting may especially play a role in the response of the predominantly calcareous grasslands of the southern Alps, where our predictions suggest increasing combined risk from drought and N deposition in the future. Anyway, owing to these climate effects on N processes, the CLs for eutrophication themselves should probably be adjusted for climate perturbations (Posch, 2002) as soon as reliable data for such adjustments become available.

Apart from alpine grasslands, our results confirm the particular sensitivity of oligotrophic habitats, such as bogs, to climate change (Essl et al., 2012) and N deposition (Bobbink et al., 1998; Bobbink et al., 2010a, 2010b) alike. Even under the most favourable combination of scenarios applied here, 43% of ‘Raised and blanket bogs’ throughout Austria will experience combined stress of climate warming and N deposition by 2050. Both alpine grasslands and bogs and mires should hence be prioritized in research and monitoring of interactive climate and nitrogen effects and respective conservation efforts.

Areas with combined risk from all three stressors were relatively rare. However, one such “hotspot” was found for ‘Broadleaved deciduous woodland’ in the Biosphere Reserve Vienna (cf. Fig. 4). Models on sensitivity of Austrian Forests had already indicated substantial potential impacts of climate change on the forests of this region (Lexer, 2001). How the combination with additional N stress will affect these ecosystems is difficult to foresee. For instance, McDonnell et al. (2014) suggest climate warming induced tree growth might lower soil N availability through aboveground immobilization, thus lowering the overall magnitude of combined effects (see also Dirnböck et al., 2017). On the other hand, an additional constraint in precipitation limits trees ability to counteract possible negative effects by increased growth, and exceedance of critical N loads may actually decrease the drought

tolerance of trees (Bobbink et al., 2010b). We emphasize that further addressing this issue is indispensable for the future health of a concerned natural reserve close to the Austrian capital and consequently air quality in Austria's largest city.

Apart from the hotspots of combined risks of at least one climate factor and N deposition, a substantially higher fraction of the studied habitats is at risk from at least one stressor. There are three issues. First, the definitions of the climatic thresholds were inherently arbitrary. However, these thresholds can be adapted depending on the purpose and required sensitivity of an assessment and can even vary between different habitats. Second, we took a very conservative approach by assuming that the EUNIS-habitat type present in a certain cell is locally represented by the syntaxonomical alliance with the lowest risk value. Thus, the results of our method particularly depend upon the quality of the underlying habitat map and will improve with it. Considerable progress has been made in some parts of Europe in providing such maps (Kuttner et al., 2015). Third, we did not account for the potential risks of increased precipitation under climate change for habitats depending on relatively dry climates (e.g. dry grasslands) in our assessment.

5. Conclusions

Empirical studies and dynamic models may evaluate in detail interactive effects of N deposition and climate change at specific sites and under given conditions. As an add-on for conservation planning and monitoring, we here propose a new method ideally suited for large-scale risk assessment. This method is an alternative to directly including N deposition effects into the empirical niche functions, which are as yet only constrained by climatic factors. This is currently in development for parts of Europe, but is still hampered by the limited availability of on-ground measurements to calibrate N-driven niche functions for a large enough number of species (Dirnböck et al., 2017; Rizzetto et al., 2016; Rowe et al., 2015). Here, our simpler method has many advantages as it allows for rapid identification of habitats and areas where targeted conservation measures must be implemented, supported by more research and monitoring.

Applying our method to Austria pinpointed hotspots of combined risks and showed that risks from future warming and drought together with N deposition particularly occur in alpine grassland habitats, bogs and mires. With excess N deposition occurring already for three decades and clear climate warming in Central Europe since the 1980ies, these combined risks potentially may cause accumulated and unexpected loss of biodiversity in the future (Essl et al., 2015). Since management has limited potential for the reduction of eutrophication in vast areas such as the alpine grassland belt (Jones et al., 2017), significant emission reduction of both reactive N as well as greenhouse gases is necessary to avoid this scenario.

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Appendix A. Supplementary data

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